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AN EXPERIMENTAL STUDY OF THE BEHAVIOR OF AMPHIPODS WITH RESPECT TO LIGHT IN- TENSITY, DIRECTION OF RAYS AND METABOLISM.

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I. INTRODUCTION.

The object of this study was to determine the effect of reagents and conditions affecting metabolism upon the reactions of amphipods to intensity and direction of light rays. The reagents and treatments used were potassium cyanide, chloretone, starvation and lowered oxygen content. All experiments were performed in the laboratory either upon amphipods just brought in, or upon those kept in captivity from one to ten weeks.

Three species of amphipods found in the vicinity of Chicago were used in the experiments, namely, a swift stream species, *Gammarus faciatu*s (Say); a sluggish river and lake species, *Hyalella knickerbockeri* (Bate); and a pond species, *Eucran-gonyx gracilis* (Smith).

(A) *Methods*.—In all the experiments a dark room was used. The special apparatus was a light grader, designed and first used by Yerkes ('02) and described with diagrams by Mast ('11, p. 61)

and Shelford ('14). In the light grader the animals are kept during experiments in a small rectangular tank having glass sides. A false bottom in this tank allows running water to pass through and thus keep the water the animals are in at constant temperature. Midway between this tank and the nernst lamp in the grader there is a partition having a triangular aperture and this aperture is covered by a lens. By this means an intense field of light is made to fall upon one end of the small tank when the latter is placed at the focal point of the lens. This field of intensity shades off to darkness in the opposite end of the tank because of the triangular opening, thus making an intensity gradient. The light which passes through the glass sides of the small tank is reflected by mirrors to a dead black wall in another part of the grader.

When ready for the experiment the animals were placed in the small tank, usually three at a time, and allowed to remain in darkness for a short time to recover from the shock of handling. Then the light was flashed upon the tank and immediately the animals were released from the glass tube with which they had been confined. Every thirty seconds the relative positions of the animals in the tank were recorded. In part of the experiments 40 readings each were taken, the first 10 of which were discarded because of the excitement of the animals due to handling and to the flashing of the intense light upon them. In the remaining experiments 25 readings each, with the first five discarded, were found to be enough to give typical results.

In each set of experiments the tank occupied by the animals was placed in three different positions: position 1, at right angles to the direction of the light rays; position 2, at an angle of 45° to the direction of rays with the *dark* end nearer to the lamp; position 3, at an angle of 45° to the direction of rays with the *light* end nearer to the lamp. The animals were first released in the field of intense light and a series of readings taken; then the same animals were released in the dark end, and oftentimes also in the place of medium light, the readings being repeated in each case.

About 50 of the 257 experiments performed were eliminated because of avoidable errors in preliminary work. The animals

were selected at random from the pan when experimented upon and the reactions under different conditions were compared.

When treating the animals with KCN and the other reagents they were kept in shallow glass dishes with a glass cover plate sealed on with vaseline to prevent evaporation. In the experiments with these animals the same solutions which they had been kept in were used in order to avoid the possibility of any stimulation which might occur by changing to tap water. The untreated amphipods were kept, and experimented on, in tap water. Filtered tap water was used in working with starved animals.

It was necessary, first, to establish a standard for the normal reactions of untreated amphipods, and then to compare with this any different reactions of treated amphipods. The series of experiments on untreated amphipods, by which the standard for normal reactions was established, form a good control series with which to compare the reactions of treated amphipods. Untreated amphipods were considered normal if they were negative to intense light when the tank was in position 1 or position 3. They were also considered normal if they were positive to intense light when the tank was in position 2. The reaction of the animals in position 2 of the tank shows that the direction of rays has a stronger influence than light intensity, for, though negative to intense light, in no case in any of the experiments with untreated animals with the tank in this position did the majority remain in the dark area. We may conclude from this that amphipods are negative to direction of rays. With treated amphipods these normal reactions were reversed in many experiments as will be shown later.

It was impossible to separate the influence of light intensity from that of direction of rays in cases where the tank was in position 3. Normally with the tank in this position both light intensity and direction of rays force the animals to the dark end. The percentage of those seeking the dark end when the tank was in this position was much greater than when the tank was at right angles to the rays, showing again the negative reaction to the direction of rays. The ray direction does not function when the tank is at right angles to it, except possibly to force

the animals to the side of the tank farthest away from the lamp. Comparative figures which will be given later indicate at least that ray direction may force the animals to the side farthest from the lamp. Possibly the data as regards light intensity *vs.* ray direction has been over-emphasized.

We can base our conclusions definitely on the effect of the direction of rays only upon reactions with the tank set in position 2. The standard for this experimental work is based therefore both upon light intensity and direction of rays.

II. RESPONSES OF UNTREATED AMPHIPODS TO LIGHT INTENSITY AND TO DIRECTION OF RAYS.

Table I. shows the reactions of untreated amphipods when the tank was at right angles to the direction of light rays (position 1). Not only are the three species compared but also the stock kept in the laboratory several weeks is compared with that freshly brought in.

TABLE I.

UNTREATED AMPHIPODS.

Experimental Tank at Right Angles to Direction of Rays (Position 1).

Species.	In Capacity.	Total Readings.	Normal Reactions.				Reversed Reactions.			
			Readings.	% +.	% α.	% -.	Readings.	% +.	% α.	% -.
<i>Gammarus</i>	4 weeks	150	150	37	21	42	60	0	0	0
	2 days	120	60	27	19	54		54	26	20
<i>Hyalella</i>	4 weeks	130	130	16	7	77		0	0	0
	1 day	150	150	13	10	77		0	0	0
<i>Eucrangonyx</i> . . .	6 weeks	150	150	13	11	76		0	0	0
	1 day	60	60	20	7	73		0	0	0

+ indicates a positive reaction, α an indifferent reaction, - a negative reaction.

The strongest negative reaction to intensity is shown by the *Hyalella* and *Eucrangonyx* species, 73 to 77 per cent. This means that in the 150 half minute readings, *e. g.*, *Eucrangonyx* 6 weeks stock, only 13 per cent. of the animals were found in the area of intense light, 11 per cent. in the medium or dim light and 76 per cent. in the dark area. Although 13 per cent. were in the field of intense light at the time the readings were taken, yet, in most instances, the stay in that area was but momentary. If the animals in their "random movements" or "busy explora-

tions" entered the field of intense light they were plainly stimulated and usually darted back quickly to the dark area.

The typical reaction for the species, negative to intense light, was that given by a majority of the untreated amphipods in the series of readings taken, and the group was considered to give reversed reactions only when a majority, in a series of readings, was found in the region of greatest light intensity. Such a reversal was found with one group of *Gammarus*, fresh stock, where in 60 readings the majority, 54 per cent., were found to be positive to intense light, while but 20 per cent. were negative, at the time of the readings. Another group of *Gammarus* fresh stock, however, was just as strongly negative to intensity. In this case of reversed reaction the animals remained in the intensity field much more constantly than did those of other groups which showed strong negative reactions. These few reversals with *Gammarus* may be due to the intense light, or to some factor not recognized. Mast ('11) has reported cases where long continued or increased light intensity has reversed the phototactic reactions of certain animals. The terrestrial form of amphipods, *Orchestia agilis*, is negatively phototactic when first exposed to light, but becomes positively phototactic with bright light, the stronger the light the quicker the reaction.

When the tank was placed in an oblique position so that it was at an angle of 45° to the direction of light rays with the dark end nearer the lamp (position 2), the majority of reactions in all the experiments performed were normal. As stated above, this normal reaction is based upon both light intensity and direction of rays, and as the direction of rays exerts a stronger influence than does intensity, the animals were forced to the light end of the tank, when the tank was in this position, and so appear positive to intense light. The percentages of normal reactions (positive readings), with the tank in position 2, are not so high as in position 1 (negative readings). This undoubtedly is due to the fact that the influences of intensity and direction of rays were working against each other when the tank was in position 2.

The position of the tank was again changed so that it was at an angle of 45° to the direction of rays with the light end nearer the lamp (position 3). In all except one series of readings,

namely with *Gammarus* fresh stock, the large majority of reactions were normal, that is, negative to light intensity and to direction of rays. In this one case of reversed reaction with *Gammarus* the same animals were used as in Table I., where a reversed reaction is shown. With the tank in position 3 the percentages of normal readings were much higher than is true of the other positions of the tank. This is due to the combined action of intensity and ray direction in position 3, both together forcing more animals to the dark or negative end of the tank than does intensity alone when the tank is in position 1. The average percentage is $78\frac{1}{3}$ negative reaction for position 3 of the tank and $66\frac{1}{2}$ for position 1.

In the above three positions of the tank a larger percentage of animals freshly obtained was negative both to light intensity and to direction of rays, in all cases except one series of readings, than were the animals kept in the laboratory for several weeks. Some factor or factors associated with long captivity apparently had an effect in lessening the negative responses of the amphipods to intensity and to direction of rays. Possibly the metabolic rate was depressed by laboratory conditions causing a tendency to a reversal.

Table II. shows the percentage of experiments giving normal

TABLE II.

UNTREATED AMPHIPODS.

*Experimental Tank at Right Angles and at Oblique Angles to Direction of Rays
(Positions 1, 2 and 3).*

	No. of Experiments Performed.	No. of Readings.	Normal Reactions, Per Cent. of Experiments.	Reversed Reactions, Per Cent. of Experiments.
Laboratory stock.....	33	1,174	100	0
Fresh stock.....	27	990	85.1	14.9
Totals.....	60	2,164	93.3	6.7

and reversed reactions with all untreated amphipods, both with the tank at right angles and at angles of 45° to the direction of rays.

III. RESPONSES OF TREATED AMPHIPODS TO LIGHT INTENSITY AND TO DIRECTION OF RAYS.

(A) *Potassium Cyanide*.—Only stock kept in the laboratory for some weeks was used in these experiments. Three different strengths of cyanide were tried, N/100,000, N/125,000, and N/150,000. Both reversed and normal responses occurred with all three. Probably the N/100,000 is not too strong for work with these animals and quicker results may be obtained with this strength. The animals were kept in the different solutions for varying lengths of time, one to nine days.

In Table III. the reactions of the three species are shown with the tank in position 2. In this case the *Hyalella* gave no majority of reversals in any series of readings, though the other two species showed strong reversals. Where the animals were exposed a longer time, as with *Eucrangonyx*, all the experiments gave a majority of reversed reactions. When the tank was in position 1 or 3 the results were very similar to those in position 2.

TABLE III.

AMPHIPODS TREATED WITH POTASSIUM CYANIDE.

Experimental Tank at an Angle of 45° to Direction of Rays with the Dark End Nearer the Lamp (Position 2).

Species.	In Capacity.	Total Readings.	Normal Reactions.				Reversed Reactions.				Time Exposed.
			Readings.	% +.	% α.	% -.	Readings.	% +.	% α.	% -.	
<i>Gammarus</i> ...	6 weeks	320	270	61	27	12	50	0	43	57	1-3 days
<i>Hyalella</i>	2 weeks	180	180	73	5	22	0	0	0	0	2-3 "
<i>Eucrangonyx</i> .	9½ weeks	90		0	0	0	90	26	22	52	2-9 "

(B) *Chloretone*.—For these experiments a solution of 0.0025 per cent. was used, which was strong enough to give a very perceptible odor of chloretone. The animals were kept in this solution from 8 to 12 days before experimenting. This length of time exposed undoubtedly was a factor in causing many more reversed reactions than with other treatments.

When the tank was in position 1 the *Gammarus* showed a much larger per cent. of reversed than normal reactions, but the other two species were all normal in the majority of readings. In the other two positions of the tank all three species had strong

reversals, and the *Hyaella* and *Eucrangonyx* gave no majority of normal reactions in any series of readings. See Table IV.

TABLE IV.

AMPHIPODS TREATED WITH CHLORETONE.

Experimental Tank at an Angle of 45° to Direction of Rays with the Light End Nearer the Lamp (Position 3).

Species.	In Captivity.	Total Readings.	Normal Reactions.				Reversed Reactions.				Time Exposed.
			Readings.	% +.	% α.	% -.	Readings.	% +.	% α.	% -.	
<i>Gammarus</i> ...	8-9 weeks	150	60	35	10	55	90	56	17	27	8-12 days
<i>Hyaella</i>	4 "	60		0	0	0	60	95	2	3	9 "
<i>Eucrangonyx</i> .	1½ "	60		0	0	0	60	57	7	36	9 "

(C) *Starvation*.—Amphipods from each habitat were kept in filtered tap water and starved from 4 to 14 days before experimenting. Reversed reactions occurred with all three species, some after short treatment, others only after long treatment. Table V. shows reversed reactions with *Hyaella* and *Eucrangonyx* when the tank was in position 2. *Gammarus* gave reversed reactions with the tank in positions 1 and 3, but the majority were normal with the tank in position 2.

TABLE V.

STARVATION TREATMENT.

Experimental Tank at an Angle of 45° to Direction of Rays with the Dark End Nearer the Lamp (Position 2).

Species.	In Captivity.	Total Readings.	Normal Reactions.				Reversed Reactions.				Time Exposed.
			Readings.	% +.	% α.	% -.	Readings.	% +.	% α.	% -.	
<i>Gammarus</i> ...	6½ weeks	60	60	56	19	25		0	0	0	4 days
<i>Hyaella</i>	7 "	120	60	71	5	24	60	38	21	41	6-9 "
<i>Eucrangonyx</i> .	1½-3 "	120	60	40	21	39	60	32	17	51	5-14 "

(D) *Low Oxygen Content*.—The oxygen content of tap water was reduced by using a machine, devised by Shelford and Allee ('13), for deaërating water by a process of heating and then cooling to the required temperature. The oxygen content was reduced in some experiments to as low as 0.79 c.c. per liter. The dish containing the amphipods was filled with this low oxygen water and the cover sealed down with vaseline. Amphipods began to die after an exposure of about one day to low

oxygen content of from 0.79 c.c. to 1.51 c.c. per liter. Only *Gammarus* gave a majority of reversed reactions in any series of readings (see Table VI.), and this took place with the tank in positions 1 and 3. The other two species gave no majority of reversed reactions in any position of the tank.

TABLE VI.

LOW OXYGEN CONTENT.

Experimental Tank at Right Angles to Direction of Rays (Position 1).

Stock.	Total Readings.	Normal Reactions.				Reversed Reactions.				Time Exposed.	C.c. of O ₂ per Liter.
		Readings.	% +.	% α.	% -.	Readings.	% +.	% α.	% -.		
<i>Gammarus</i> ...	120	60	0	5	95	60	67	11	22	19 hrs.	0.79
<i>Hyalella</i>	60	60	34	18	48		0	0	0	17 "	1.51
<i>Eucrangonyx</i> .	60	60	23	18	59		0	0	0	22½ "	0.99

In Table VII. the percentage of experiments is given showing normal and reversed reactions with all treated amphipods, both with the tank at right angles and at angles of 45° to the direction of rays.

TABLE VII.

TREATED AMPHIPODS.

All Three Species. Tank in Positions 1, 2 and 3.

Treatment.	No. of Experiments Performed.	No. of Readings.	Normal Reactions, Per Cent. of Experiments.	Reversed Reactions, Per Cent. of Experiments.
Potassium cyanide.....	54	1,520	72.3	27.7
Chloretone.....	27	810	44.5	55.5
Starvation.....	29	900	69.0	31.0
Low oxygen.....	22	720	68.2	31.8

Table VIII. shows that the percentage of reversals in the three species is quite different under the same treatment. Also, in the same species, the percentage of reversals varies for each reagent used.

TABLE VIII.

TREATED AMPHIPODS.

Reversed Reactions only.

	<i>Gammarus</i> , Per Cent. of Experiments.	<i>Hyalella</i> , Per Cent. of Experiments.	<i>Eucrangonyx</i> , Per Cent. of Experiments.
Reversed reaction with KCN.....	39.3	5.5	33.3
" " " Chloretone....	60.0	66.6	33.3
" " " Starvation....	66.6	18.2	25.0
" " " Low Oxygen....	36.3	50.0	0.0

IV. SIDES OF THE EXPERIMENTAL TANK, IN RELATION TO THE LAMP, OCCUPIED BY THE AMPHIPODS.

At each reading, when the position of the animals in relation to intensity was taken, their position in relation to the sides of the tank was also taken. The object was to determine, if possible, whether the direction of rays influenced the animals to seek the side of the tank farthest from the lamp.

The results are shown in Table IX. The readings have no reference to the dark end of the tank. In positions 1 and 2 the largest per cent. of the animals was found on the side of the tank farthest from the lamp, while in position 3 the majority were found on the side nearest the lamp. This is not conclusive, however, and these lateral positions in the tank may be due only to "random excursions" or "busy explorations" that Holmes ('01) speaks of as characteristic of active animals. Possibly the animals were reacting towards their own shadow, in positions 1 and 2, rather than to ray direction. It is interesting to note that there is very little difference in the results between treated and untreated amphipods.

In none of the experiments was there evidence of orientation either to light intensity or to direction of rays.

TABLE IX.

TANK AT RIGHT ANGLES TO DIRECTION OF RAYS (POSITION 1).

	Side Farthest from Lamp.	Median Position.	Side Nearest to Lamp.
Untreated Amphipods.....	48.5%	11.3%	40.2%
Treated ".....	49.2	14.9	35.9

TANK AT ANGLE OF 45° TO DIRECTION OF RAYS WITH DARK END NEARER THE LAMP (POSITION 2).

Untreated Amphipods.....	52.9%	7.7%	39.4%
Treated ".....	49.2	12.6	38.2

TANK AT ANGLE OF 45° TO DIRECTION OF RAYS WITH LIGHT END NEARER THE LAMP (POSITION 3).

Untreated Amphipods.....	35.7%	11.5%	52.8%
Treated ".....	37.9	11.7	50.4%

V. CONCLUSIONS AND DISCUSSION.

(A) *Summary*.—1. In an experimental tank set at right angles to the direction of light rays and graded from intense light to darkness, pond, stream and river amphipods, as a group, seek the dark area, therefore are negative to light intensity.

2. When the same tank is set obliquely, at an angle of 45° , to the direction of rays with the dark end nearer the lamp, the amphipods are forced to the light area, even though they are negative to intense light. The stimulus of the direction of rays, to which the amphipods react negatively, has a stronger effect than the stimulus of light intensity.

3. If the experimental tank is set at an angle of 45° to the direction of rays so that the light end is nearer the lamp, normal amphipods, as a group, seek the dark end. In this case the direction of rays exerts the same stimulating effect as light intensity in forcing the animals to the dark area. This again shows a negative reaction to intensity and to direction of rays. A larger percentage show negative reaction, with the tank in this position, than when the tank is at right angles to the light rays.

4. When treated with certain depressing agents many of these amphipods become reversed in their reactions to light intensity and to direction of rays.

5. Freshly obtained amphipods give a larger percentage of negative reactions, both to intensity and direction of rays, than do amphipods which have been kept in the laboratory for some time.

6. In these experiments there is no evidence of orientation of amphipods either to light intensity or to direction of rays.

7. Changes in the metabolic processes (physiological states) of the amphipods were undoubtedly the cause of reversed reactions in this series of experiments.

Some of the above results have been obtained also by other investigators. Holmes ('01) says that all aquatic amphipods studied by him were negatively phototactic, although three species of land amphipods studied were positively phototactic. Loeb ('04), writing about experiments on *Gammarus pulex* and other animals, says that "whatever increases the activity tends to increase the positive reaction to light, while anything which

tends to quiet the animals tends to make them negative." He adds also that the *Gammarus pulex*, which is negative to light, can be made positive by adding to the water a little carbon dioxid, hydrochloric, oxalic or acetic acid, ether, chloroform, paraldehyde, alcohol, esters and all ammonium salts. Boracic acid, according to Loeb, does not reverse these amphipods, but Jackson ('10), in repeating Loeb's experiments, but using *Hyaella knickerbockeri*, found that a saturated solution of boracic acid does cause a reversal, the same as the other reagents. Jackson also found that some other acids and some alkalies produce the same effect. These reversals took place, however, only when he dropped the animals into the solution, for when he put the animals into distilled water and gradually added the chemicals no reversals took place.

McCurdy ('13) says that "sunlight modifies the normal physiological changes taking place in protoplasm, checking some of the processes and probably accelerating the others. A starfish in the light moves to the shade because of disturbance by light of his metabolism." A part of this disturbance was due to there being "less CO₂ given off by the starfish when it was put in the sunlight."

(B) *Metabolism, Physiological States and Reactions*.—Before answers can be given to many questions that arise, much more work along these lines must be done. Other methods and treatments must be used, such as high oxygen content, caffeine, acids, alkalies, carbon dioxid content, etc.

From the data obtained from this series of experiments it is evident that the responses of aquatic amphipods, like those of many other animals experimented upon, are related directly to the physiological state or condition of the animal. Anything which disturbs the rate of metabolism of the animal alters the response to stimuli. Allee ('12) with isopods, Child ('10) with planaria, Wodsedalek ('11) with may-fly nymphs, and other investigators have found this to be true.

In these experiments on amphipods then, the reversed reactions are caused by some change in the metabolic processes of the animals. Potassium cyanide depresses the metabolic processes by decreasing oxidation. Oxidation is decreased by

decreasing the ability of the tissues to take up oxygen. Chloretone is a soporific and has a depressing or inhibiting effect upon certain metabolic processes. Starvation decreases metabolism by removing the material to be oxidized. Such reagents and treatments are known to have specific effects on metabolism and they also cause reversals in phototaxis, therefore the responses are related to the metabolic rate of the animal.

Jennings ('04) says that physiological states are the most important determining factors in reaction and behavior. By physiological states he means the varying physiological conditions as distinguished from permanent anatomical conditions. Can we be sure that such physiological states do exist? If we subject animals to the same external conditions and give the same stimulus, and the animals react differently, then the difference must be due to variations in internal conditions; else the reactions would always be the same. A stimulus changes the physiological state of the animal as a whole, and this change in physiological state induces a certain type of reaction.

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